



A novel, validated, and plant height-independent QTL for spike extension length is associated with yield-related traits in wheat

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Abstract

Key message A novel, stably expressed, and plant height-independent QTL for spike extension length on 5AS was identified and validated in different populations using a newly developed and tightly linked KASP marker.

Abstract As an important component of plant height (PH), spike extension length (SEL) plays a significant role in formation of an ideotype in wheat. Despite the fact that numerous loci for SEL in wheat have been reported, our knowledge on PH-independent loci remains to be limited. In this study, two recombinant inbred line (RIL) populations genotyped using the Wheat55K SNP were used to detect quantitative trait loci (QTL) controlling SEL across six environments. A total of 30 QTL for SEL were detected in these two RIL populations, and four of them, i.e., *QSEL.sicau-2CN-4D*, *QSEL.sicau-2SY-4B.2*, *QSEL.sicau-2SY-4D.1*, and *QSEL.sicau-2CN-5A*, were stably expressed. Genetic and conditional QTL analysis showed that the first three were significantly associated with PH, while the last one, *QSEL.sicau-2CN-5A*, is independent of PH. Comparison of genetic and physical maps suggested that only *QSEL.sicau-2CN-5A* located on chromosome arm 5AS is likely a novel QTL. A Kompetitive Allele-Specific PCR (KASP) marker, *KASP-AX-110413733*, tightly linked to this novel QTL was developed to successfully confirm its effect in three different genetic populations. Further, in the interval where *QSEL.sicau-2CN-5A* was located on ‘Chinese Spring’ wheat reference genome, three promising genes mainly expressed in wheat stem were predicated and they all encode the cytochrome P450 that was demonstrated to be closely associated with SEL elongation in rice. In addition, significant correlations between SEL and PH, spikelet number per spike, and thousand-grain weight were also detected. Altogether, our results broaden our understanding on genetic basis of SEL and will be useful for marker-based selection of lines with different SELs and fine mapping the novel and PH-independent QTL *QSEL.sicau-2CN-5A*.

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Introduction

An ideotype in wheat has greater potential in yield increase given its advantages with improved photosynthesis, reduced lodging, and enhanced ability of allocation of assimilation to grain (Yao and Zhu 1998; Berry et al. 2007; Cui et al. 2011; Semenov et al. 2013). Spike extension length (SEL), part of plant height (PH), is the distance from the base of the panicle to the petiole of the flag leaf (Yu et al. 2014) and plays an important role in formation of an ideotype (Zhang et al. 2017). The longer SEL can increase airflow in panicle and decrease air humidity, and thus reducing Fusarium Head Blight (FHB) (Ma et al. 2017). However, a higher PH usually increased with the addition of SEL may lead to the bending or falling of the panicles thus resulting in yield and quality

decline (Bridgemohan and Bridgemohan 2014). Therefore, only a suitable SEL can lead to the high yield of wheat.

Numerous studies associated with SEL have been reported in rice. For example, the overexpression of *CYP94C2b* may increase the number of internode elongated cells (Kurotani et al. 2015). The cytochrome P450 monooxygenase regulated the accumulation of gibberellins (GAs) to affect the elongation of SEL (Zhu et al. 2006; Zhang et al. 2008b). However, in wheat, few studies have been reported on SEL (Ma et al. 2006; Qiao et al. 2007; Ku et al. 2015; Zhang et al. 2018; Ji et al. 2019). For example, the QTL for SEL on the chromosome 5D increased SEL by 0.16 mm (Tian et al. 2015). Five stable QTL have important effects on the development of plant height components (Zhang et al. 2017). In addition, six new QTL for controlling SEL were identified using genome-wide association analysis (Li et al. 2019b).

SEL is closely associated with the development of inflorescence, and it is an important organ for studying the transportation system in wheat (Reynolds et al. 2009; Dixon et al. 2020). However, many QTL controlled SEL were significantly affected by PH, making it difficult to precisely dissect the effect of SEL on wheat yield in breeding (Law et al. 1978; Hoogendoorn et al. 1990). Furthermore, our knowledge on the genetic basis and regulation mechanism about SEL in wheat is largely unknown. Thus, it is essential to detect and identify QTL for SEL that is not affected by PH.

In addition, it is widely reported that the multivariable conditional analysis for analyzing the contributions of component traits to a complex trait was used to detect whether a given QTL is affected by other traits (Cui et al. 2011; Yu et al. 2014; Tao et al. 2019). In this study, we thus used this method to identify possible QTL for SEL that is not dependent on PH. Our results revealed four stable QTL controlling SEL identified in two recombinant inbred line (RIL) populations based on the genetic maps constructed using the Wheat55K SNP array. A new Kompetitive Allele-Specific PCR (KASP) marker was developed to further validate a novel QTL that was independent of PH in three populations. Possible candidate genes associated with the novel QTL were predicated as well. These results laid a foundation for molecular marker-based selection of wheat lines with different SELs and cloning the novel and stable QTL.

Materials and methods

Plant materials

Five populations were used in this study. They were 20828/Chuannong 16 (CN16; 2CN, 199 F₆ RILs including two parents) (Liu et al. 2018), 20828/SY95-71 (2SY, 128 F₇ RILs including two parents) (Liu et al. 2020), S849-8/CN16

(SCN, 217 F₅ lines including two parents), MTL7/CN16 (M7C, 128 F₃ lines including two parents), and MZ-5/CN16 (MC, 116 F₃ lines including two parents). 20828, SY95-71, S849-8, MTL7, and MZ-5 are advanced wheat lines that have been used in wheat breeding. CN16 is a commercial variety (Ma et al. 2019a). 2CN and 2SY RIL populations were used for QTL mapping and the other three were used for validating the identified PH-independent QTL.

Phenotypic evaluation

The 2CN and 2SY populations were grown in six different environments for phenotypic evaluation: Wenjiang (103° 51' E, 30° 43' N) in 2018 and 2019 (2018WJ, and 2019WJ), Chongzhou (103° 38' E, 30° 32' N) in 2018 and 2019 (2018CZ, and 2019CZ), Ya'an (103° 0' E, 29° 58' N) in 2018 and 2019 (2018YA and 2019YA) of Sichuan Province in China. SCN, M7C, and MC populations were grown in Chongzhou in 2020. A random block design was used for all of the trials. Each line was planted in a single 1.5 m row with 0.3 m between rows, and the sowing density was 15 seeds per row with 0.1 m between plants within a row (Liu et al. 2018). All field trials were well irrigated and managed in accordance with local standard practices (Ma et al. 2020).

At least three representative and disease-free plants in each line were selected to measure the PH, SL, spikelet number per spike (SNS), thousand-grain weight (TGW), and SEL according to a previous study (Tao et al. 2019). Among these traits, data of PH (Li et al. 2019a; Liu et al. 2020), SL (Li et al. 2019a), SNS (Ma et al. 2019a; Liu et al. 2020), and TGW (Ma et al. 2019c, 2020; Liu et al. 2020) from 2CN and 2SY were retrieved from our previous studies (Table S1).

Genetic map construction and QTL analysis

Two genetic linkage maps constructed using the Wheat55K SNP array were used in this study. In the 2CN population, the markers were distributed in 34 linkage groups with an average interval of 0.84 cM between adjacent markers (Liu et al. 2018; Ma et al. 2019b). In the 2SY population, the markers were distributed in 38 linkage groups and the genetic map covered a total genetic distance of 4,273.03 cM with mean, minimum, and maximum marker densities of 1.69, 0.70, and 5.33 cM/marker, respectively (Liu et al. 2020). We used IciMapping 4.1 based on Biparental Populations (BIP) module with the inclusive composite interval mapping (ICIM, <https://www.isbreeding.net/software/?type=detail&id%20=18>) for QTL detection in 2CN and 2SY populations. The minimal logarithm of odds (LOD) score to accept the presence of a QTL was set at 2.5 (Lin et al. 1996). QTL was named based on the International Rules of Genetic Nomenclature (<https://wheat.pw.usda>

gov/ggpages/wgc/98/Intro.htm). ‘Sicau’ represents Sichuan Agricultural University.

Conditional QTL analysis

Conditional QTL analysis was usually to interpret the relationship between complex traits and components (Cui et al. 2011). In conditional QTL analysis, the LOD value was decreased or increased significantly but was greater than 2.5 indicating that the QTL was partially, but not adequately, correlated with other traits; the LOD value was reduced to less than 2.5 meaning that the QTL was thoroughly contributed by other traits (Zhu 1995; Cui et al. 2011). The conditional phenotypic values (SELIPH) were obtained by QGASStation2.0.exe software (Cui et al. 2011). IciMapping 4.1 was also used to identify the conditional QTL with conditional phenotypic values.

Physical intervals of the novel QTL and comparison with previously reported QTL

The physical location of the novel QTL’s flanking markers on *T. aestivum* cv. Chinese Spring or CS [International Wheat Genome Sequencing Consortium (IWGSC) RefSeq v1.0] was obtained from our previous studies (Liu et al. 2018; Ma et al. 2019b).

The probe sequences of flanking markers for each previously reported QTL or genes related to SEL on 4B, 4D and 5A were used for BLASTn against (*E*-value of 1e-5) the genome assemblies of CS [(IWGSC) RefSeq v1.0; <https://urgi.versailles.inra.fr/download/iwgsc/>] (IWGSC 2018) to get their physical locations. The UniProt (<https://www.uniprot.org/>) was used to analyze the annotations and functions of a given gene. Additionally, the expression patterns of the predicated candidate genes of the novel QTL were obtained from the Triticeae Multi-omics Center (<https://202.194.139.32/expression/index.html>) and WheatExp (<https://wheat.pw.usda.gov/WheatExp/#>) using published data from IWGSC (2014) and IWGSC (2018).

Marker development and QTL validation

To validate the identified novel QTL, we converted a SNP marker *AX-110413733* into a KASP maker as previously described (Ma et al. 2019a). Eighty lines randomly selected from three validation populations (SCN, M7C, MC), respectively, were used to do genotyping using this KASP marker. The amplification reactions were performed in a total volume of 10 µl containing 0.75 µl of template DNA, 5 µl of SsoFast EvaGreen mixture (Bio-Rad, Hercules, CA, USA), and 1.4 µl of mixture forward and reverse primers (*KASP-AX-110413733F*: GAAGGTGACCAAGTTCATGCTTTG TTTTGGATTCGGGTTTTTC, *KASP-AX-110413733H*: GAA

GGTCGGAGTCAACGGATTTTGTGGATTCGGGTT TTG, *KASP-AX-110413733R*: GCAAGTTCAAAATCG AAAT), and DNase/RNase-free water up to the final value. CFX96™ Real-Time System made in Singapore was used to genotype. The PCR reaction procedure was as follows: 15 min at 94 °C, 40 cycles of 20 s at 94 °C, and 60 s at 61 °C–55°C (drop 0.6 °C, per cycle).

According to the genotype of the KASP marker in the three validation populations, the lines were divided into two groups: (1) lines with homozygous alleles from either of S849-8, MTL7, and MZ-5; (2) lines with homozygous alleles from CN16. Lines with heterozygous genotype were abandoned. Student’s *t* test ($P < 0.01$) was also used to evaluate the SEL between the above two groups.

Data analysis

The average values of SEL of more than three representative plants from each line were used in the succeeding analysis. The best linear unbiased prediction (BLUP) of target traits in different environments (Smith et al. 1998) and the broad-sense heritability (h^2) were calculated using SAS V8.0 (SAS Institute, Cary, NC, USA; <https://www.sas.com>). IBM SPSS Statistic 26 (SPSS, Chicago, IL, USA; <https://en.wikipedia.org/wiki/SPSS>) was used to perform Student’s *t* test ($P < 0.05$) and correlation analysis of different phenotype values in different environments. Lines carrying different alleles at the major QTL from 2CN and 2SY populations were selected based on the genotype of its flanking markers and further compared for the SEL traits using Student’s *t* test ($P < 0.05$).

Results

Phenotypic variation of SEL traits

Significant differences between 20828 and CN16 for 2CN population (Fig. 1a) and between 20828 and SY95-71 for 2SY population (Fig. 1b) were observed. CN16 and SY95-71 had consistently and significantly higher values for SEL than 20828 (Table 1). The SEL ranged from 1.10 cm to 27.94 cm in the 2CN population and from 1.61 cm to 21.30 cm in the 2SY population (Table 1). The standard deviation (SD) of 2CN and 2SY populations ranged from 1.59 to 3.74 and from 2.21 to 4.21, respectively. The h^2 of 2CN and 2SY populations were 0.88 and 0.94, respectively, indicating SEL was mainly controlled by genetic factors (Table 1).

Moreover, the frequency distribution of SEL in different environments was indicative of multigenic inheritance (Fig. S1). Significant and positive correlations for SEL were detected among six different environments, BLUP dataset and SELIPH ($P < 0.01$). The correlation coefficients ranged

Fig. 1 Phenotypes of the parents and selected lines. **a** The spike extension length (SEL) of 20828, CN16, and selected lines from the 2CN population; **b** the SEL of 20828, SY95-71, and selected lines from the 2SY population (scale bar = 5 cm)

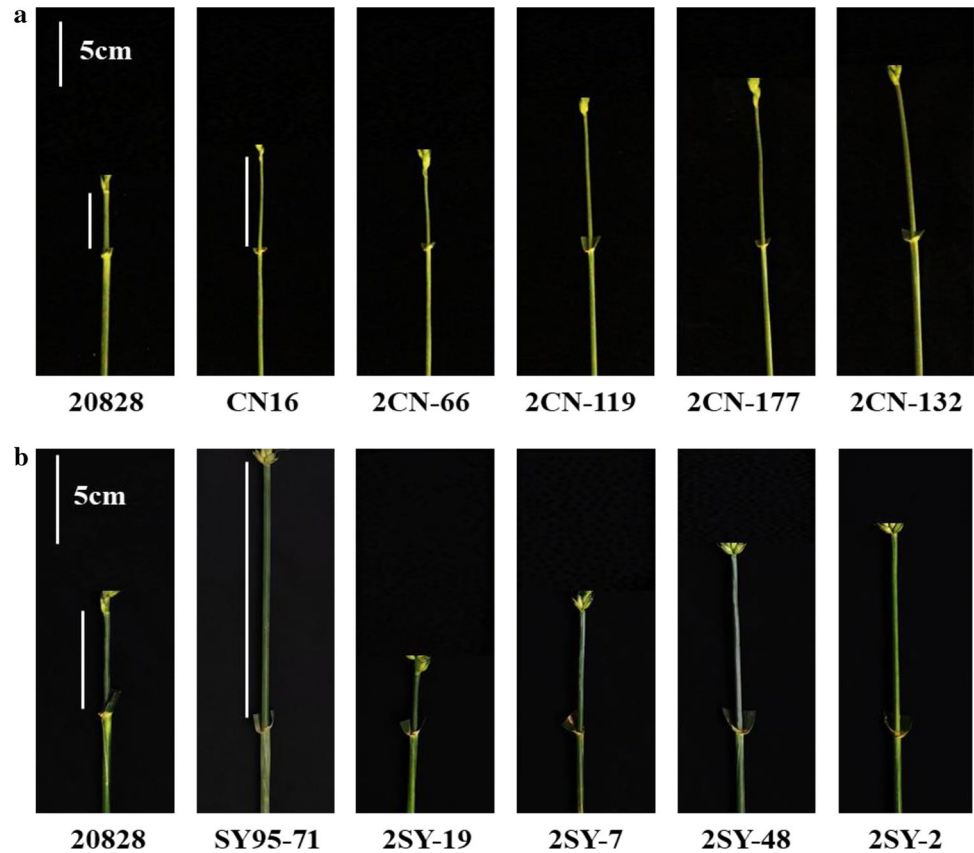


Table 1 Phenotypic variation of SEL in 2CN and 2SY populations grown in different environments

Environment	Parents		2CN-RIL						2SY-RIL			
	20828	CN16	20828	SY95-71	Min–Max	Mean	SD	h^2	Min–Max	Mean	SD	h^2
2018WJ	7.77	11.68**	7.55	17.35**	2.18–27.94	10.58	3.56		3.56–21.30	11.89	3.68	
2018CZ	7.86	11.17*	6.11	12.68*	1.36–19.95	9.55	3.02		2.35–19.22	10.06	4.02	
2018YA	7.12	8.02	7.62	12.53**	1.42–19.83	8.52	3.38		1.61–18.94	9.14	3.72	
2019WJ	7.93	9.55*	7.27	12.56**	1.10–27.88	10.05	3.74		2.15–19.89	9.86	3.15	
2019CZ	7.12	12.39**	7.19	12.83**	1.66–22.78	9.68	3.26		1.80–18.12	9.08	3.77	
2019YA	7.10	9.80**	7.07	12.17**	3.43–17.40	9.88	2.73		1.68–21.11	9.67	4.21	
BLUP	7.58	10.40	7.46	12.97	2.31–21.08	9.66	2.86	0.88	3.92–18.46	9.89	3.12	0.94
SELIPH	7.60	11.15	7.76	12.87	6.05–16.40	9.73	1.59		5.55–15.35	9.89	2.21	

RIL recombinant inbred lines, BLUP best linear unbiased prediction, h^2 broad-sense heritability; Environments: Year+Location: WJ (Wenjiang); CZ (Chongzhou); YA (Ya'an); SELIPH: the conditional phenotypic values; 2CN: 20828/CN16; 2SY: 20828/SY95-71; SD: standard deviation; **Significant at $P < 0.01$, *Significant at $P < 0.05$

from 0.493 to 0.950 for the 2CN population and from 0.583 to 0.940 for the 2SY population (Table 2).

Correlation analysis between SEL and yield-related traits

Phenotypic correlations between SEL and other yield-related traits are listed in Table 3. Significant and positive correlations ($P < 0.05$) between SEL and PH and TGW, and

significant and negative correlation ($P < 0.01$) between SEL and SNS were observed in both 2CN and 2SY populations (Table 3, Fig. 2).

QTL for SEL

A total of 30 QTL for SEL were detected in 2CN (13 QTL) and 2SY (17 QTL) populations (Table 4). They were located on chromosomes: 1B, 1D, 2A, 2B, 2D, 3D, 4A, 4B, 4D, 5A,

Table 2 Correlation of SEL between different environments in 2CN and 2SY populations

	2CN	2018WJ	2018CZ	2018YA	2019WJ	2019CZ	2019YA	BLUP	SELIPH	2SY
2018WJ			0.867**	0.821**	0.822**	0.786**	0.850**	0.917**	0.667**	2018WJ
2018CZ	0.878**			0.782**	0.804**	0.771**	0.828**	0.882**	0.593**	2018CZ
2018YA	0.858**	0.828**			0.763**	0.795**	0.829**	0.881**	0.641**	2018YA
2019WJ	0.863**	0.781**	0.792**			0.863**	0.862**	0.906**	0.583**	2019WJ
2019CZ	0.855**	0.780**	0.836**	0.858**			0.854**	0.896**	0.642**	2019CZ
2019YA	0.577**	0.548**	0.676**	0.577**	0.589**			0.940**	0.665**	2019YA
BLUP	0.950**	0.906**	0.933**	0.919**	0.923**	0.748**			0.710**	BLUP
SELIPH	0.682**	0.610**	0.638**	0.662**	0.697**	0.493**	0.682**			SELIPH

2CN: 20828/CN16; 2SY: 20828/SY95-71. The below triangle represents the correlation among different environments in 2CN population and the above triangle represents the correlation among different environments in 2SY population; SELIPH: the conditional phenotypic values; **Significant at $P < 0.01$, *Significant at $P < 0.05$

Table 3 Effects of spike extension length (SEL) on other agronomic traits

Trait	PH	SNS	SL	TGW
2CN-SEL	0.656**	- 0.305**	- 0.047	0.169*
2SY-SEL	0.704**	- 0.303**	- 0.023	0.184*

The influence of SEL on other agronomic traits was evaluated by the BLUP dataset. PH plant height; SNS spikelet number per spike; SL spike length; TGW thousand-grain weight; **Significant at $P < 0.01$, *Significant at $P < 0.05$

5D, 6A, 6B, 6D, and 7A. Four of them were stably detected in at least three environments (Table 4).

In the 2CN population, two stable QTL *QSEL.sicau-2CN-4D* and *QSEL.sicau-2CN-5A* were detected. *QSEL.sicau-2CN-4D*, detected in four environments as well as the BLUP dataset, was located on chromosome arm 4DS. It explained between 5.17% and 8.74% of the phenotypic variance (Table 4, Fig. 3a). *QSEL.sicau-2CN-5A* with 5.31%–10.20% of the phenotypic variance, as a major locus, was detected in four environments as well as the BLUP dataset and SELIPH on chromosome arm 5AS (Table 4, Fig. 3b). The positive alleles of these two stable QTL were both contributed by CN16. The remaining 11

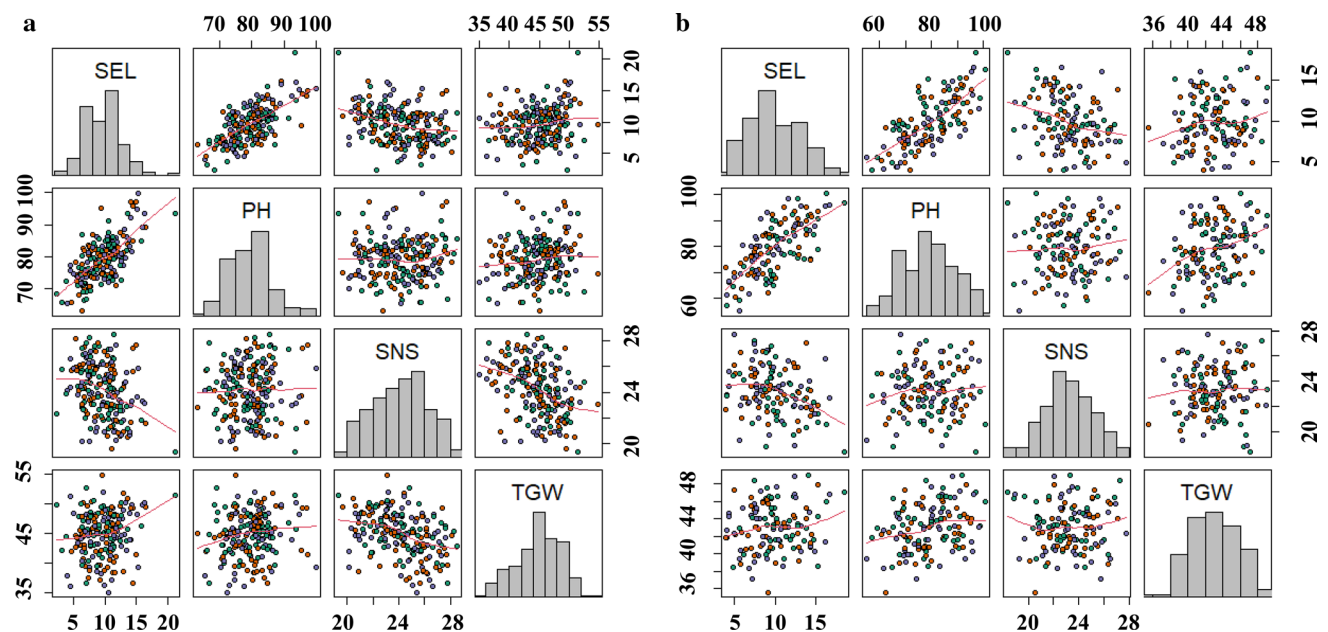


Fig. 2 Effects of spike extension length (SEL) on other traits. Effects of SEL on plant height (PH), spikelet number per spike (SNS), and thousand-grain weight (TGW) in 2CN (a) and 2SY (b) populations, respectively. The relationships of SEL, PH, SNS, and TGW were

evaluated by the BLUP dataset. The histogram of each trait was shown in the main diagonal. The scatter diagram of different traits was shown below and above the main diagonal

Table 4 Quantitative trait loci (QTL) for spike extension length (SEL) identified from different environments in 2CN and 2SY populations

QTL	Environment	Chromosome	Interval (cM)	Left Marker	Right Marker	LOD	PVE (%)	Add
<i>QSEL.sicau-2CN-1B</i>	2018CZ	1B	35.23–37.17	<i>AX-110976825</i>	<i>AX-89435736</i>	3.29	6.73	0.75
<i>QSEL.sicau-2CN-2A.1</i>	BLUP	2A	41.38–42.33	<i>AX-108858837</i>	<i>AX-110617782</i>	3.20	5.61	– 0.66
<i>QSEL.sicau-2CN-2A.2</i>	SELIPH	2A	39.76–40.26	<i>AX-108908958</i>	<i>AX-111658249</i>	4.56	9.71	– 0.48
<i>QSEL.sicau-2CN-2D</i>	2019CZ	2D	42.70–44.26	<i>AX-109822660</i>	<i>AX-110816831</i>	2.89	6.74	– 0.78
<i>QSEL.sicau-2CN-4A</i>	BLUP	4A	56.52–60.51	<i>AX-109285973</i>	<i>AX-110030140</i>	3.55	6.38	0.71
<i>QSEL.sicau-2CN-4D</i>	2018WJ	4D	37.82–39.16	<i>AX-110400439</i>	<i>AX-110046962</i>	3.72	8.74	– 0.95
	2018YA	4D	37.82–39.16	<i>AX-110400439</i>	<i>AX-110046962</i>	2.69	5.49	– 0.78
	2019WJ	4D	37.82–39.16	<i>AX-110400439</i>	<i>AX-110046962</i>	3.48	8.41	– 1.10
	2019CZ	4D	37.82–39.16	<i>AX-110400439</i>	<i>AX-110046962</i>	3.19	6.91	– 0.79
	BLUP	4D	37.82–39.16	<i>AX-110400439</i>	<i>AX-110046962</i>	3.14	5.17	– 0.64
<i>QSEL.sicau-2CN-5A</i>	2018WJ	5A	13.97–15.31	<i>AX-110413733</i>	<i>AX-95012249</i>	3.05	7.14	– 0.85
	2018CZ	5A	13.97–15.31	<i>AX-110413733</i>	<i>AX-95012249</i>	2.62	5.31	– 0.66
	2018YA	5A	13.97–15.31	<i>AX-110413733</i>	<i>AX-95012249</i>	3.42	7.09	– 0.87
	2019CZ	5A	13.97–15.31	<i>AX-110413733</i>	<i>AX-95012249</i>	4.18	9.25	– 0.90
	BLUP	5A	13.97–15.31	<i>AX-110413733</i>	<i>AX-95012249</i>	3.30	5.58	– 0.65
	SELIPH	5A	13.97–15.31	<i>AX-110413733</i>	<i>AX-95012249</i>	4.91	10.20	– 0.48
<i>QSEL.sicau-2CN-5D</i>	2018YA	5D	18.98–21.55	<i>AX-110085499</i>	<i>AX-109561083</i>	3.33	7.88	0.93
<i>QSEL.sicau-2CN-6A.1</i>	2018WJ	6A	51.54–52.44	<i>AX-109463428</i>	<i>AX-111048864</i>	2.85	7.21	– 0.85
<i>QSEL.sicau-2CN-6A.2</i>	2018CZ	6A	62.98–66.39	<i>AX-109283360</i>	<i>AX-110442638</i>	3.60	7.54	– 0.80
	2019CZ	6A	62.98–66.39	<i>AX-109283360</i>	<i>AX-110442638</i>	2.90	6.47	– 0.76
	BLUP	6A	62.98–66.39	<i>AX-109283360</i>	<i>AX-110442638</i>	3.95	6.85	– 0.74
<i>QSEL.sicau-2CN-6D.1</i>	2018WJ	6D	89.56–97.33	<i>AX-109088524</i>	<i>AX-108978672</i>	2.63	6.99	0.84
	2018YA	6D	89.56–97.33	<i>AX-109088524</i>	<i>AX-108978672</i>	2.82	6.78	0.85
	BLUP	6D	89.56–97.33	<i>AX-109088524</i>	<i>AX-108978672</i>	3.59	6.75	0.72
<i>QSEL.sicau-2CN-6D.2</i>	2019WJ	6D	61.84–71.92	<i>AX-111480830</i>	<i>AX-108814900</i>	3.23	7.87	1.05
<i>QSEL.sicau-2CN-7A</i>	2018CZ	7A	40.22–41.23	<i>AX-111604641</i>	<i>AX-110518554</i>	3.01	6.18	– 0.72
<i>QSEL.sicau-2SY-1D</i>	SELIPH	1D	99.43–100.23	<i>AX-111504007</i>	<i>AX-110389611</i>	4.62	13.67	– 0.78
<i>QSEL.sicau-2SY-2B.1</i>	2018YA	2B	26.66–31.16	<i>AX-109391223</i>	<i>AX-108806563</i>	3.40	11.80	– 1.31
<i>QSEL.sicau-2SY-2B.2</i>	2018YA	2B	159.57–160.94	<i>AX-109447372</i>	<i>AX-108826010</i>	2.54	8.27	1.09
<i>QSEL.sicau-2SY-2D</i>	SELIPH	2D	0–2.29	<i>AX-109687504</i>	<i>AX-109007985</i>	2.56	7.27	– 0.58
<i>QSEL.sicau-2SY-3D.1</i>	2019YA	3D	8.29–9.04	<i>AX-111438110</i>	<i>AX-110365829</i>	4.50	9.26	– 1.32
	SELIPH	3D	7.29–8.29	<i>AX-109333856</i>	<i>AX-111438110</i>	4.10	11.93	– 0.74
<i>QSEL.sicau-2SY-3D.2</i>	2019YA	3D	18.63–22.39	<i>AX-89662133</i>	<i>AX-110197171</i>	2.67	5.34	1.00
<i>QSEL.sicau-2SY-4A</i>	2019WJ	4A	78.97–81.1	<i>AX-109391536</i>	<i>AX-108899858</i>	3.31	8.61	– 1.12
<i>QSEL.sicau-2SY-4B.1</i>	2019CZ	4B	0–0.41	<i>AX-110928817</i>	<i>AX-111620391</i>	3.25	10.39	– 0.94
<i>QSEL.sicau-2SY-4B.2</i>	2018CZ	4B	0.95–4.92	<i>AX-111573292</i>	<i>AX-111233094</i>	6.58	14.54	– 1.61
	2019WJ	4B	0.95–4.92	<i>AX-111573292</i>	<i>AX-111233094</i>	5.79	16.92	– 1.59
	2019YA	4B	0.95–4.92	<i>AX-111573292</i>	<i>AX-111233094</i>	4.92	11.26	– 1.47
	BLUP	4B	0.95–4.92	<i>AX-111573292</i>	<i>AX-111233094</i>	4.56	13.22	– 1.17
<i>QSEL.sicau-2SY-4D.1</i>	2018WJ	4D	63.45–77.48	<i>AX-110572006</i>	<i>AX-109230716</i>	7.98	18.45	– 2.17
	2018CZ	4D	63.45–77.48	<i>AX-110572006</i>	<i>AX-109230716</i>	4.63	11.81	– 1.43
	2018YA	4D	63.45–77.48	<i>AX-110572006</i>	<i>AX-109230716</i>	3.37	11.88	– 1.31
	BLUP	4D	63.45–77.48	<i>AX-110572006</i>	<i>AX-109230716</i>	3.82	12.31	– 1.12
<i>QSEL.sicau-2SY-4D.2</i>	2019YA	4D	55.14–59.33	<i>AX-94547815</i>	<i>AX-110527441</i>	5.23	11.34	– 1.47
<i>QSEL.sicau-2SY-5A</i>	2018WJ	5A	11.34–14.90	<i>AX-108892891</i>	<i>AX-109512380</i>	4.75	8.48	– 1.47
<i>QSEL.sicau-2SY-5D</i>	2019WJ	5D	5.33–6.45	<i>AX-111460807</i>	<i>AX-110625313</i>	2.85	7.34	– 1.04
<i>QSEL.sicau-2SY-6B.1</i>	2019CZ	6B	121.37–122.31	<i>AX-109935603</i>	<i>AX-108954574</i>	4.22	13.96	– 1.09
	BLUP	6B	121.37–122.31	<i>AX-109935603</i>	<i>AX-108954574</i>	2.94	7.50	– 0.87
<i>QSEL.sicau-2SY-6B.2</i>	2019YA	6B	120.83–121.34	<i>AX-110996963</i>	<i>AX-108757761</i>	5.15	10.74	– 1.41
<i>QSEL.sicau-2SY-6D.1</i>	2018CZ	6D	106.23–140.47	<i>AX-108978672</i>	<i>AX-110364778</i>	2.95	5.78	1.02
<i>QSEL.sicau-2SY-6D.2</i>	2018CZ	6D	90.71–91.11	<i>AX-111139406</i>	<i>AX-108971696</i>	3.27	6.24	– 1.04

LOD logarithm of odds, PVE phenotype variance explained, Add additive effect of a QTL; Positive values: alleles from 20828 are increasing the trait scores, negative values: alleles from CN16 or SY95-71 are increasing the scores; BLUP best linear unbiased prediction; SELIPH the conditional phenotypic values

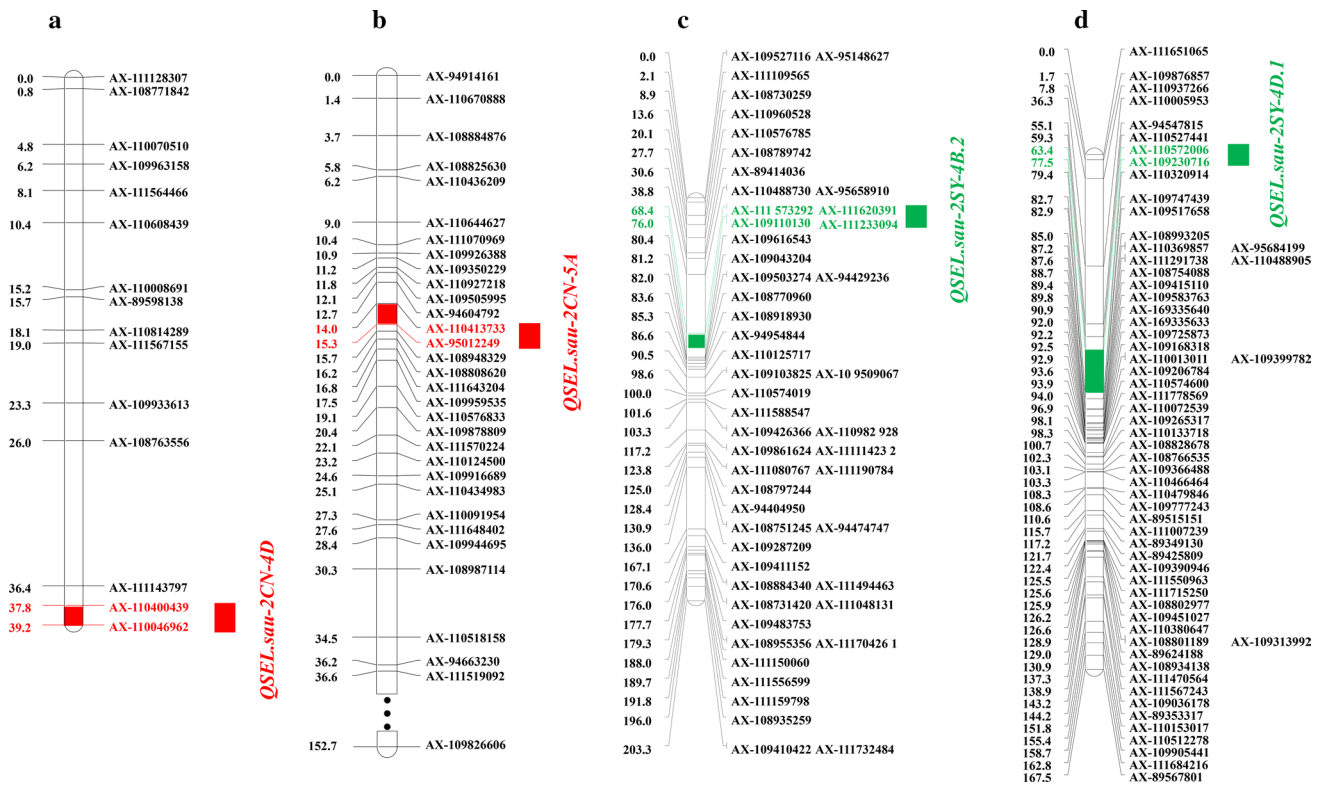


Fig. 3 Genetic maps of the stable QTL for spike extension length (SEL) identified in 2CN and 2SY populations. Genetic maps of *QSEL.sau-2CN-4D* (a), *QSEL.sau-2CN-5A* (b), *QSEL.sau-2SY-4B.2* (c), and *QSEL.sau-2SY-4D.1* (d) for SEL, respectively

QTL detected in less than three environments explained between 5.61% and 9.71% of the phenotypic variance (Table 4).

Two stable QTL *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* were also detected in the 2SY population. *QSEL.sicau-2SY-4B.2* detected in three environments as well as the BLUP dataset was located on 4BS chromosome (Fig. 3c). This locus explained between 11.26% and 16.92% of the phenotypic variance (Table 4). *QSEL.sicau-2SY-4D.1* was detected in three environments and BLUP dataset. It was located on chromosome arm 4DS and explained between 11.81% and 18.45% of the phenotypic variance (Table 4, Fig. 3d). The positive alleles of these two stable QTL were both contributed by SY95-71. The remaining 15 QTL were detected in a single environment and explained between 5.34% and 13.96% of the phenotypic variance (Table 4).

QTL \times environment (QE) interaction analysis showed that a total of 18 QTL were detected in 2CN and 2SY populations (Table S2). Fourteen of them were the same as those detected in individual environment. For example, *QSEL.sicau-2CN-4D*, *QSEL.sicau-2CN-5A*, and *QSEL.sicau-2SY-4D.1* were simultaneously detected by multi-environmental and individual environmental analyses, further indicating that they were major and stable QTL (Table S2).

Effects of *QSEL.sicau-2CN-4D* and *QSEL.sicau-2CN-5A* on SEL in the 2CN population

The positive alleles of both *QSEL.sicau-2CN-4D* and *QSEL.sicau-2CN-5A* were from CN16 (Table 4). Their effects on SEL were further analyzed in the 2CN population (Fig. 4a). Compared with those without any of the alleles increasing SEL, RILs possessing the positive allele from *QSEL.sicau-2CN-4D* significantly increased SEL by 26.69%; those possessing the positive allele from *QSEL.sicau-2CN-5A* significantly increased SEL by 22.48%; and those with the combination of *QSEL.sicau-2CN-4D* and *QSEL.sicau-2CN-5A* significantly increased SEL by up to 42.69%. In addition, RILs with the combination of positive alleles of *QSEL.sicau-2CN-4D* and *QSEL.sicau-2CN-5A* increased SEL by 12.63% and 16.50%, respectively, compared to those with the positive allele of either *QSEL.sicau-2CN-4D* or *QSEL.sicau-2CN-5A* in 2CN population.

Effects of *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* on SEL in the 2SY population

The positive alleles of both *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* were from SY95-71 in 2SY population (Table 4). Their effects on SEL were analyzed as

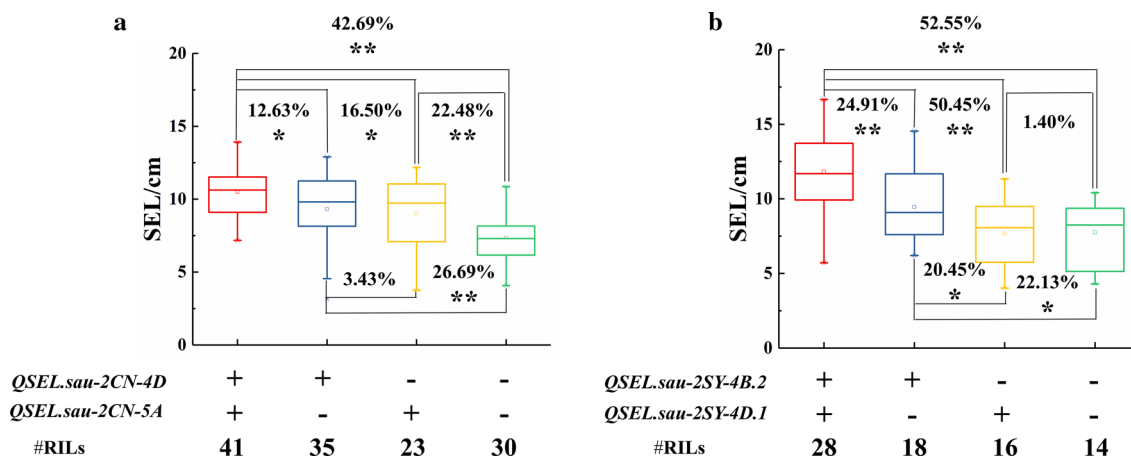


Fig. 4 Effects of *QSEL.sau-2CN-4D* and *QSEL.sau-2CN-5A* for SEL in the 2CN population (a) and those of *QSEL.sau-2SY-4B.2* and *QSEL.sau-2SY-4D.1* for SEL in the 2SY population (b). + and – represent lines with and without the positive alleles of the target

quantitative trait loci (QTL) based on the flanking marker of the corresponding QTL, respectively. **Significant at $P < 0.01$, *Significant at $P < 0.05$. Differences between the two groups were labeled above the significant levels

well (Fig. 4b). Compared with those without any of the alleles increasing SEL, RILs possessing the positive allele from *QSEL.sicau-2SY-4B.2* increased SEL by 22.13%; those with the combination of *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* significantly increased SEL by up to 52.55%. Furthermore, RILs with the combination of positive alleles of *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* significantly increased SEL by 24.91% and 50.45%, respectively, compared to those with the positive allele of either *QSEL.sicau-2SY-4B.2* or *QSEL.sicau-2SY-4D.1* in 2SY population. Besides, RILs with the positive allele of *QSEL.sicau-2SY-4B.2* increased SEL by 20.45% compared to those of *QSEL.sicau-2SY-4D.1*.

Conditional QTL analysis-based determination of relationships between SEL and PH

SEL is an important part of PH. Thus, theoretically, SEL is closely correlated with PH. Conditional QTL analysis was carried out to determine the genetic relationships between SEL and PH. The LOD scores of the three major QTL *QSEL.sicau-2CN-4D*, *QSEL.sicau-2SY-4B.2*, and *QSEL.sicau-2SY-4D.1* were significantly decreased below 2.5 when SEL was conditional on PH, implying they were closely related to PH (Fig. 5a, c, d). Interestingly, no significant difference was detected for the LOD score of *QSEL.sicau-2CN-5A* in 2CN population when SEL was conditional on PH (Fig. 5b). These results suggested that *QSEL.sicau-2CN-5A* was likely independent of PH.

Validation of the PH-independent QTL *QSEL.sicau-2CN-5A*

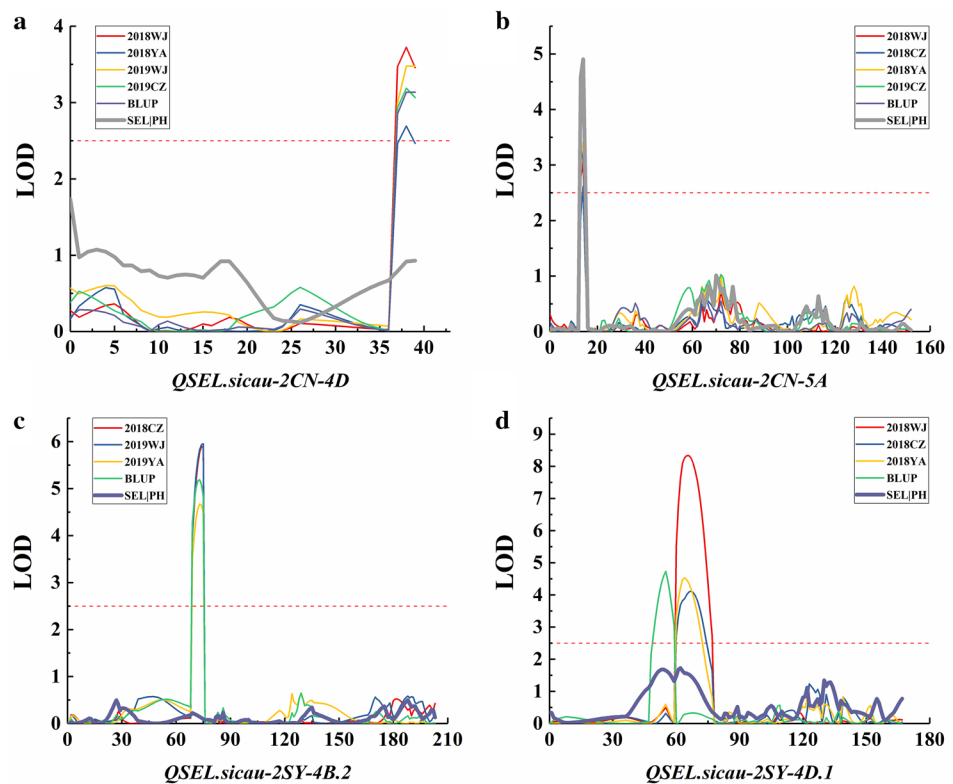
A newly developed KASP marker (*KASP-AX-110413733*) tightly linked to *QSEL.sicau-2CN-5A* was developed to validate the effects of *QSEL.sicau-2CN-5A* in three populations with different genetic backgrounds (SCN, M7C, and MC). The polymorphism between parent CN16 and the other three parents S849-8, MTL7 and MZ-5 was detected using the marker *KASP-AX-110413733*. According to the genotype (excluding heterozygotes), the lines were divided into two groups (Fig. 6a–c). As expected, Student's *t* test detected significant differences ($P < 0.01$) between them (Fig. 6d–f). The lines with positive alleles from CN16 have significantly higher values than those without these alleles, and the differences between the two groups ranged from 13.04% to 36.95% with an average of 23.43% in three validation populations.

Discussion

Correlation analysis of SEL and yield-related traits

SEL and SNS had a significant and negative correlation, indicating that there may be a competition between SEL and SNS during plant growth (Miralles et al. 1998; Bancal 2008). SEL was positively correlated with TGW, which is consistent with many previous reports (Yao et al. 2003; Ma et al. 2017). These results indicated that when plant height

Fig. 5 Stable QTL detected for spike extension length (SEL) using conditional QTL analysis method. *QSEL.sicau-2CN-4D* (a), *QSEL.sicau-2CN-5A* (b), *QSEL.sicau-2SY-4B.2* (c), and *QSEL.sicau-2SY-4D.1* (d) controlling SEL identified using unconditional and conditional QTL analysis methods. (LOD=2.5, red dotted line)



was determined, the longer SEL likely benefits the grain yield increasing. This is because SEL has a certain function of photosynthesis and temporary storage of energy and water, and thus, a longer SEL showing a longer distance between the panicle and flag leaf likely benefits the transportation of nutrients and water to seeds (Bridgemohan and Bridgemohan 2014; Ávila et al. 2017). Besides, a longer SEL was also helpful for ventilating and thus reducing the occurrence of FHB (Ma et al. 2017). Thus, a suitable SEL is likely beneficial for improving TGW.

Both of the LOD and PVE of SEL QTL on 5A indeed increased after the PH effect was removed in conditional analysis. However, according to conditional QTL analysis, no significant difference was detected for the LOD score of *QSEL.sicau-2CN-5A* in 2CN population when SEL was conditional on PH (Cui et al. 2011). Thus, *QSEL.sicau-2CN-5A* may be plant height-independent. Furthermore, there was no significant difference for PH between with and without the positive allele of *QSEL.sicau-2CN-5A* in 2CN population (Fig. S2). These results suggested that all loci controlling SEL might work together to increase PH, and thus, PH is positively correlated with SEL.

Stable QTL controlling SEL

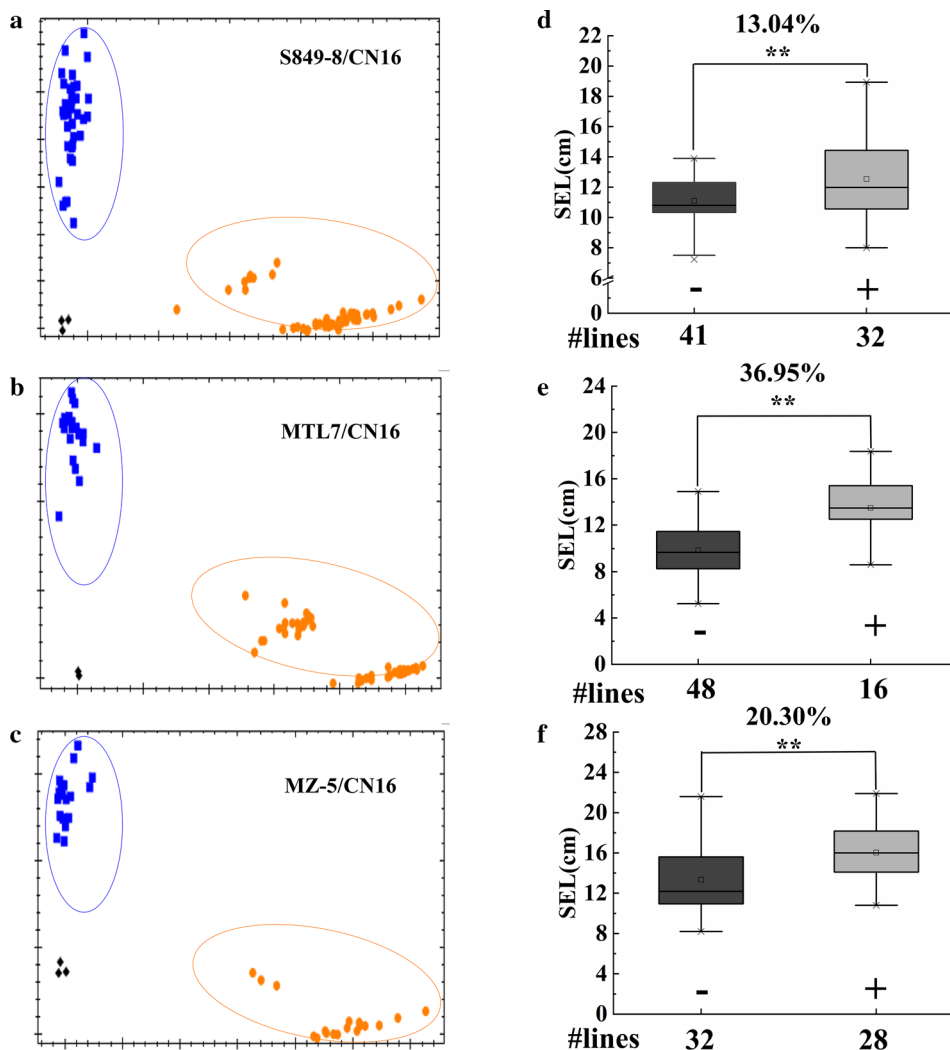
To further identify relationships between QTL detected in this study and previous studies, we compared their physical

intervals on the CS reference genome. *QSEL.sicau-2SY-4B.2* was located in the interval between 37.87 and 45.42 Mbp close to *QPel.HM.4B* (Tao et al. 2019), suggesting that they are likely alleles (Table S3). *QSEL.sicau-2CN-4D* and *QSEL.sicau-2SY-4D.1* were closely located on chromosome arm 4DS and may be allelic (Table S4). No QTL for SEL were detected on 4DS in previous studies to date. However, they were overlapped with QTL for PH (Table S4). *QSEL.sicau-2CN-5A* was located between 4.85 and 6.46 Mbp on chromosome arm 5AS (Table S5), which is different from previously reported SEL-related loci (Korzun et al. 1997; Wu et al. 2010; Jia et al. 2013; Linn et al. 2017; Zhang et al. 2017; Li et al. 2019b). These results showed that *QSEL.sicau-2CN-5A* may be a novel QTL controlling SEL identified in the present study.

Possible gene interaction between *QSEL.sicau-2SY-4B* and *QSEL.sicau-2SY-4D.1*

Two QTL controlling SEL were detected in 2SY population. When the positive allele from *QSEL.sicau-2SY-4B.2* was present only, SEL increased significantly; when the positive allele from *QSEL.sicau-2SY-4D.1* was present only, SEL increased insignificantly; however, the combination of positive alleles of *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* increased SEL significantly and extremely. Thus, we speculate that there is a gene interaction between

Fig. 6 Validation of *QSEL.sau-2CN-5A* in three populations with different genetic backgrounds. Eighty lines randomly selected from SCN, M7C, and MC populations, respectively, were used to do genotyping using the KASP marker *KASP-AX-110413733*. Fluorescence PCR typing results of the Kompetitive Allele-Specific PCR (KASP) marker *KASP-AX-110413733* in S849-8/ CN16 (SCN, **a**), MTL7/CN16 (M7C, **b**), and MZ-5/CN16 (MC, **c**) populations. Blue round represents lines with the allele of CN16 (FAM fluorescence); orange box frame represents lines with the allele of S849-8 (**a**), MTL7 (**b**), MZ-5 (**c**), respectively (HEX fluorescence); effects of *QSEL.sau-2CN-5A* in three validation populations of SCN (**d**), M7C (**e**), and MC (**f**), respectively. + and – represent lines with and without the positive alleles of the target quantitative trait loci (QTL) based on the flanking marker (*KASP-AX-110413733*) of the corresponding QTL, respectively. **Significant at $P < 0.01$; Differences between the two groups were labeled above the significant levels



the positive allele of *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1*. Yu et al. (2002) clearly demonstrated the importance of epistatic interactions in genetic bases of QTL controlling plant height in rice. Zhang et al. (2008a) showed that epistatic effects were also important for genetic bases of PH in wheat. *QSEL.sicau-2SY-4B.2* and *QSEL.sicau-2SY-4D.1* were influenced by PH. Therefore, they might be also involved in epistatic interactions between each other in 2SY population, and the positive allele of *QSEL.sicau-2SY-4D.1* can enhance the effect of *QSEL.sicau-2SY-4B.2*. However, fine mapping and map-based cloning are needed to further reveal their interaction mechanism.

Genetic relationships between SEL and PH

QSEL.sicau-2SY-4B.2 was located on chromosome 4BS (37.87–45.42 Mbp). *Rht-B1b*, an important PH-related gene, was also located on chromosome 4BS (Zhang et al. 2013). BLAST results suggested that *Rht-B1b* was located at 30.86 Mbp on CS RefSeqv.1.0 sequence (Jobson et al.

2019). Thus, *QSEL.sicau-2SY-4B.2* is not likely allelic to *Rht-B1b*. However, it is co-located with *QPh.sau.4B.1* for PH detected in the present study (Table S6) and overlapped with the PH-related QTL *QPh.nau.4B.2* (Jia et al. 2013).

Both *QSEL.sicau-2CN-4D* and *QSEL.sicau-2SY-4D.1* were located on 4DS. *Rht-D1b* as a PH gene was also located on chromosome 4DS and BLAST results suggested that *Rht-D1b* was located at 18.78 Mbp (Zhang et al. 2013). *QSEL.sicau-2CN-4D* and *QSEL.sicau-2SY-4D.1* were located in the intervals 9.56–10.38 Mbp and 19.18–37.81 Mbp, respectively. Although they were likely far from *Rht-D1b*, they were both co-located with the PH QTL detected in this study (Table S5) and overlapped with the PH-related QTL *QPh-4D* (Table S4) (Liu et al. 2014).

It is documented that the resolution of primary QTL mapping was rough due to the limited population size as well as the interference of environments (Dinka et al. 2007; Liu et al. 2018). Besides, based on different genetic backgrounds, we would be hard to rule out that *QSEL.sicau-2SY-4B.2* is affected by *Rht-B1* or *QSEL.sicau-2SY-4D.1* and

QSEL.sicau-2CN-4D are affected by *Rht-D1*. Additionally, this study clearly demonstrated that *QSEL.sicau-2SY-4B.2*, *QSEL.sicau-2CN-4D*, and *QSEL.sicau-2SY-4D.1* were indeed affected by PH using conditional QTL analysis. Therefore, in order to further reveal the relationship between the three SEL-related QTL and *Rht* genes, we need to do fine mapping and even map-based cloning work.

QSEL.sicau-2CN-5A identified by unconditional and conditional QTL analysis methods was located at 4.85–6.46 Mbp on chromosome arm 5AS. The PH-related genes *Rht-9* (Linn et al. 2017) and *Rht-12* (Sun et al. 2019) were located at 558.34 Mbp and 678.29 Mbp, respectively, on chromosome arm 5AL, being clearly far from *QSEL.sicau-2CN-5A* (Table S5).

Thus, based on correlation, conditional QTL, genetic, and physical comparison analyses, SEL was significantly and positively correlated with PH. *QSEL.sicau-2CN-4D*, *QSEL.sicau-2SY-4B.2*, and *QSEL.sicau-2SY-4D.1* may have a complex relationship with PH-related genes. While the stable QTL, *QSEL.sicau-2CN-5A*, successfully validated in three different genetic backgrounds, was not affected by PH and is worthy to be further fine mapped and used for breeding wheat variety with suitable SEL using the developed KASP marker.

The predicated genes in the interval of *QSEL.sicau-2CN-5A*

Given that the novel and stable QTL *QSEL.sicau-2CN-5A* was not dependent on PH, we thus attempt to predicate genes in the interval where this QTL was located on CS reference genome. Alignment of its flanking markers showed that it was located between 4.85 Mbp and 6.46 Mbp in the deletion bin 5AS7/10–0.98–1.00 on chromosome arm 5AS (Fig. S3). In this interval, 37 predicated genes were annotated in the CS (Table S7). Expression pattern analyses showed that 17 genes were expressed in stem and the other 20 genes were not expressed in stem (Fig. S4). Further, 3 genes (*TraesCS5A01G008700*, *TraesCS5A01G008800* and *TraesCS5A01G008900*) had significantly higher expression levels in stem than other genes (Fig. S4) (IWGSC 2018). Interestingly, all of the three annotated genes encoded cytochrome P450 and they had the highest expression in stem at different growth stages (Fig. S5) (IWGSC 2018).

It was widely reported that cytochrome P450 was associated with the elongation of SEL. For example, *Eui* gene, a GA catabolism gene encoding cytochrome P450 monooxygenase was related to accumulation of active GAs in the uppermost internode thus affecting SEL in rice (Ma et al. 2006; Zhu et al. 2006; Zhang et al. 2008b). Another example is that the overexpression of cytochrome P450 enzyme, CYP94C2b, can modulate jasmonate metabolism and then increase the number of elongated cells in the uppermost

internode to elongate SEL in rice (Kurotani et al. 2015). In addition, *OsDWARF48*, a gene encoding cytochrome P450, might control the SEL by regulating the synthesis and signal pathways of brassinosteroids in rice (Zhen et al. 2018).

Therefore, we speculated that the three genes (*TraesCS5A01G008700*, *TraesCS5A01G008800* and *TraesCS5A01G008900*) encoding cytochrome P450 were likely closely related to SEL in wheat and they were useful in our following work of fine mapping and cloning of this locus.

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Author contributions statement CL carried out the entire research and participated in drafting this manuscript. HPT and WL participated in phenotype measurement and data analysis. XMZ, YM, and MD participated in fieldwork and data analysis. YXL and QTJ assisted with data collection and analysis. GYC, JRW, PFQ, ZEP, and YFJ performed data processing, QTL analysis and manuscript revision. YMW and YLZ discussed results and revised the manuscript. XJL initiated the project, guided the study, and revised the manuscript. JM designed the experiments, guided the entire study, participated in data analysis, wrote and extensively revised this manuscript. All authors participated in the research and approved the final manuscript.

Compliance with ethical standards

Conflict of interest All authors declare that there is no conflict of interest.

Ethical standards All experiments and data analyses were conducted in Sichuan. All authors contributed to the study and approved the final version for submission. The manuscript has not been submitted to any other journal.

References

- Ávila L, E., Zerpa AJ, Santiago LS, (2017) Stem photosynthesis and hydraulics are coordinated in desert plant species. *New Phytol* 216:1119–1129
- Bancal P (2008) Positive contribution of stem growth to grain number per spike in wheat. *Field Crop Res* 105:27–39
- Berry PM, Sylvesterbradley R, Berry S (2007) Ideotype design for lodging-resistant wheat. *Euphytica* 154:165–179
- Bridgemohan P, Bridgemohan SHR (2014) Evaluation of anti-lodging plant growth regulators on the growth and development of rice (*Oryza sativa*). *J Cereals Oilseeds* 5:12–16
- Cui F, Li J, Ding A, Zhao C, Wang L, Wang X, Li S, Bao Y, Li X, Feng D (2011) Conditional QTL mapping for plant height with respect to the length of the spike and internode in two mapping populations of wheat. *Theor Appl Genet* 122:1517–1536
- Dinka SJ, Campbell MA, Demers T, Raizada MN (2007) Predicting the size of the progeny mapping population required to positionally clone a gene. *Genetics* 176:2035–2054

- Dixon L, Pasquariello M, Boden S (2020) *TEOSINTE BRANCHED1* regulates height and stem internode length in bread wheat (*Triticum aestivum*). *J Exp Bot*:eraa252
- Hoogendoorn J, Rickson J, Gale M (1990) Differences in leaf and stem anatomy related to plant height of tall and dwarf wheat (*Triticum aestivum* L.). *J Plant Physiol* 136:72–77
- IWGSC (2014) A chromosome-based draft sequence of the hexaploid bread wheat (*Triticum aestivum*) genome. *Science* 345:1251788
- IWGSC (2018) Shifting the limits in wheat research and breeding using a fully annotated reference genome. *Science* 361:eaar7191
- Ji H, Han C, Lee G, Jung K, Kang D, Oh J, Oh H, Cheon K, Kim S, Choi I (2019) Mutations in the microRNA172 binding site of SUPERNUMERARY BRACT (SNB) suppress internode elongation in rice. *Rice* 12:1–14
- Jia H, Wan H, Yang S, Zhang Z, Kong Z, Xue S, Zhang L, Ma Z (2013) Genetic dissection of yield-related traits in a recombinant inbred line population created using a key breeding parent in China's wheat breeding. *Theor Appl Genet* 126:2123–2139
- Jobson E, Johnston R, Oiestad A, Martin J, Giroux M (2019) The impact of the wheat *Rht-B1b* semi-dwarfing allele on photosynthesis and seed development under field conditions. *Front Plant Sci* 10:51
- Korzun V, Röder M, Worland A, Börner AJPB (1997) Intrachromosomal mapping of genes for dwarfing (*Rht12*) and vernalization response (*Vrn1*) in wheat by using RFLP and microsatellite markers. *Plant Breed* 116:227–232
- Ku L, Cao L, Wei X, Su H, Tian Z, Guo S, Zhang L, Ren Z, Wang X, Zhu Y (2015) Genetic dissection of internode length above the uppermost ear in four RIL populations of maize (*Zea mays* L.). *G3: Genes, Genomes, Genetics* 5:281–289
- Kurotani KI, Hattori T, Takeda S (2015) Overexpression of a CYP94 family gene *CYP94C2b* increases internode length and plant height in rice. *Plant Signal Behav* 10:e1046667
- Law C, Snape J, Worland A (1978) The genetical relationship between height and yield in wheat. *Heredity* 40:133–151
- Li C, Ma J, Liu H, Ding P, Yang C, Zhang H, Qin N, Lan X (2019a) The wheat55K SNP based detection of QTL for spike length and plant height in wheat. *J Triticeae Crop* 131(11):1284–1292 (in Chinese)
- Li F, Wen W, Liu J, Zhang Y, Cao S, He Z, Rasheed A, Jin H, Zhang C, Yan J (2019b) Genetic architecture of grain yield in bread wheat based on genome-wide association studies. *BMC Plant Biol* 19:168
- Lin H, Qian H, Zhuang J, Lu J, Min S, Xiong Z, Huang N, Zheng K (1996) RFLP mapping of QTLs for yield and related characters in rice (*Oryza sativa* L.). *Theor Appl Genet* 92:920–927
- Linn T, Bachir D, Chen L, Hu Y (2017) Effects of gibberellic acid responsive dwarfing gene *Rht9* on plant height and agronomic traits in common wheat. *Am J Agric Fores* 5:102–111
- Liu G, Jia L, Lu L, Qin D, Zhang J, Guan P, Ni Z, Yao Y, Sun Q, Peng H (2014) Mapping QTLs of yield-related traits using RIL population derived from common wheat and Tibetan semi-wild wheat. *Theor Appl Genet* 127:2415–2432
- Liu J, Luo W, Qin N, Ding P, Zhang H, Yang C, Mu Y, Tang H, Liu Y, Li W (2018) A 55 K SNP array-based genetic map and its utilization in QTL mapping for productive tiller number in common wheat. *Theor Appl Genet* 131(11):2439–2450
- Liu J, Tang H, Qu X, Liu H, Li C, Tu Y, Li S, Habib A, Mu Y, Dai S, Deng M, Jiang Q, Liu Y, Chen G, Wang J, Chen G, Li W, Jiang Y, Wei Y, Lan X, Zheng Y, Ma J (2020) A novel, major, and validated QTL for the effective tiller number located on chromosome arm 1BL in bread wheat. *Plant Mol Biol*. 104:173–185
- Ma H, Zhang S, Ji L, Zhu H, Yang S, Fang X, Yang R (2006) Fine mapping and in silico isolation of the *EU11* gene controlling upper internode elongation in rice. *Plant Mol Biol* 60:87–94
- Ma J, Sun M, Ding P, Luo W, Zhou X, Yang C, Zhang H, Qin N, Yang Y, Lan X (2017) Genetic identification of QTL for neck length of spike in wheat. *J of Triticeae Crop* 37(3):319–324 (in Chinese)
- Ma J, Ding P, Liu J, Li T, Zou Y, Habib A, Mu Y, Tang H, Jiang Q, Liu Y, Chen G, Wang J, Deng M, Qi P, Li W, Pu Z, Zheng Y, Wei Y, Lan X (2019a) Identification and validation of a major and stably expressed QTL for spikelet number per spike in bread wheat. *Theor Appl Genet* 132:3155–3167
- Ma J, Qin N, Cai B, Chen G, Ding P, Zhang H, Yang C, Huang L, Mu Y, Tang H, Liu Y, Wang J, Qi P, Jiang Q, Zheng Y, Liu C, Lan X, Wei Y (2019b) Identification and validation of a novel major QTL for all-stage stripe rust resistance on 1BL in the winter wheat line 20828. *Theor Appl Genet* 132:1363–1373
- Ma J, Zhang H, Li S, Zou Y, Li T, Liu J, Ding P, Mu Y, Tang H, Deng M (2019c) Identification of quantitative trait loci for kernel traits in a wheat cultivar Chuannong16. *BMC Genet* 20:77
- Ma J, Tu Y, Zhu J, Luo W, Liu H, Li C, Li S, Liu J, Ding P, Habib A (2020) Flag leaf size and posture of bread wheat: genetic dissection, QTL validation and their relationships with yield-related traits. *Theor Appl Genet* 133:297–315
- Miralles D, Katz S, Colloca A, Slafer G (1998) Floret development in near isogenic wheat lines differing in plant height. *Field Crop Res* 59:21–30
- Qiao B, Wang Y, Zhu X, Hong D (2007) QTL analysis of the uppermost internode length in rice under different growing environments. *Heredity* 29:1001–1007
- Reynolds M, Foulkes M, Slafer G, Berry P, Parry M, Snape J, Angus W (2009) Raising yield potential in wheat. *J Exp Bot* 60:1899–1918
- Semenov AM, Stratonovitch P (2013) Designing high-yielding wheat ideotypes for a changing climate. *Food Energy Secur* 2:185–196
- Smith SE, Kuehl RO, Ray IM, Hui R, Soleri D (1998) Evaluation of simple methods for estimating broad-sense heritability in stands of randomly planted genotypes. *Crop Sci* 38:1125–1129
- Sun L, Yang W, Li Y, Shan Q, Ye X, Wang D, Yu K, Lu W, Xin P, Pei Z, Guo X, Liu D, Sun J, Zhan K, Chu J, Zhang A (2019) A wheat dominant dwarfing line with *Rht12*, which reduces stem cell length and affects gibberellic acid synthesis, is a 5AL terminal deletion line. *Plant J* 97:887–900
- Tao Y, Yi X, Lin Y, Wang Z, Wu F, Jiang X, Liu S, Deng M, Ma J, Chen G (2019) Quantitative trait locus mapping for panicle exertion length in common wheat using two related recombinant inbred line populations. *Euphytica* 215:104
- Tian J, Deng Z, Zhang K, Yu H, Jiang X, Li C (2015) Genetic analysis of main physiological and morphological traits. Springer, pp 351–443
- Wu X, Wang Z, Chang X, Jing R (2010) Genetic dissection of the developmental behaviours of plant height in wheat under diverse water regimes. *J Exp Bot* 61:2923–2937
- Yao R, Zhu W (1998) The correlation analysis of the stem traits and lodging in wheat. *J Guangxi Agric Univ* 17(16–18):23 (in Chinese)
- Yao J, Yao G, Wang S, Yang X (2003) Inheritance of neck length of spike and its breeding value in wheat. *J Guangxi Agric Univ*:16–18 (in Chinese)
- Yu M, Mao S, Chen G, Pu Z, Wei Y, Zheng Y (2014) QTLs for uppermost internode and spike length in two wheat RIL populations and their effect upon plant height at an individual QTL level. *Euphytica* 200:95–108
- Yu SB, Li JX, Xu CG, Tan YF, Li XH, Zhang Q (2002) Identification of quantitative trait loci and epistatic interactions for plant height and heading date in rice. *Theor Appl Genet* 104:619–625
- Zhang K, Tian J, Zhao L, Wang S (2008a) Mapping QTLs with epistatic effects and QTL x environment interactions for plant height using a doubled haploid population in cultivated wheat. *J Genet Genomics* 35:119–127

- Zhang Y, Zhu Y, Peng Y, Yan D, Li Q, Wang J, Wang L, He Z (2008b) Gibberellin homeostasis and plant height control by *EUI* and a role for gibberellin in root gravity responses in rice. *Cell Res* 18:412–421
- Zhang J, Dell B, Biddulph B, Drake-Brockman F, Walker E, Khan N, Wong D, Hayden M, Appels R (2013) Wild-type alleles of *Rht-B1* and *Rht-D1* as independent determinants of thousand-grain weight and kernel number per spike in wheat. *Mol breeding* 32:771–783
- Zhang N, Fan X, Cui F, Zhao C, Zhang W, Zhao X, Yang L, Pan R, Chen M, Han J (2017) Characterization of the temporal and spatial expression of wheat (*Triticum aestivum* L.) plant height at the QTL level and their influence on yield-related traits. *Theor Appl Genet* 130:1235–1252
- Zhang W, Li Z, Fang H, Zhang M, Duan L (2018) Analysis of the genetic basis of plant height-related traits in response to ethylene by QTL mapping in maize (*Zea mays* L.). *PLoS one* 13:e0193072
- Zhen L, Qingguo W, Jiaowen P, Wei L, Center BR (2018) Functional analysis of height regulation of cytochrome P450 gene *OsD-WARF48* in Rice. *Shandong Agricul Sci*:1–9 (in Chinese)
- Zhu J (1995) Analysis of conditional genetic effects and variance components in developmental genetics. *Genetics* 141:1633–1639
- Zhu Y, Nomura T, Xu Y, Zhang Y, Peng Y, Mao B, Hanada A, Zhou H, Wang R, Li P, Zhu X, Mander LN, Kamiya Y, Yamaguchi S, He Z (2006) ELONGATED UPPERMOST INTERNODE encodes a cytochrome P450 monooxygenase that epoxidizes gibberellins in a novel deactivation reaction in rice. *Plant Cell* 18:442–456

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